

Is mining the seabed bad for mollusks?

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ABSTRACT

Up to three miles below the ocean surface, deep-sea hydrothermal vents are home to a community of extraordinary mollusks. In an environment without light, under intense pressure and volcanic heat, many gastropods and bivalves living directly on the vent chimneys show adaptations that have driven important scientific breakthroughs. For example, the famous “scaly-foot” gastropod, *Chrysomallon squamiferum*, has hard scales on its foot with a crystalline iron coating that has inspired novel defensive armor designs. This iconic species has only been reported from three sites in the Indian Ocean, each site hundreds of miles apart and only around half the size of a football field. Two of these three sites are already designated under international exploration licenses for deep-sea mining, to extract rare minerals from the vent chimneys. Economic and political pressures to exploit the seabed are advancing much faster than scientific exploration, putting these vent ecosystems and their molluscan residents at risk.

conditions represent specific challenges or adaptive pressures, which manifest in shell forms that are distinctly different than shallow-water species more commonly seen in shell collections: aphotic conditions below 1000 m or less result in a lack of shell pigmentation (Abbott, 1985), and calcium limitation at depths below 3000–4000 m (Morse et al., 2007) results in typically thin and fragile shells. Aesthetics combined with the expense and technical challenges of deep-sea exploration mean that the shells of deep-sea species are, unusually for mollusks, not generally available on the commercial market.

Access to study deep-sea habitats principally depends on large-scale ocean going research vessels equipped with specialized sampling equipment. Such infrastructure is generally only available through support from government funding of major nations, and indeed most deep-sea exploration focuses on geology, oceanography, climate change, and many other aspects besides sampling benthic animals such as mollusks. The large-scale investment and funding required, and the rarity of these samples, ethically demand that all such materials should be held permanently in public collections and preserved for further research and education.

The ocean floor remains largely unexplored: perhaps 10% of the seafloor has been mapped by ship-borne instrumentation and far less has been sampled biologically (Charette and Smith, 2010). Ongoing sampling of deep-sea communities continues to uncover new species, even in areas that are relatively well studied like the NW Atlantic (Grassle and Maciolek, 1992). However, the deep-sea is biologically nutrient-limited, and many species appear to live in very low densities. So deep-sea species may rely on strong dispersal mechanisms to find sufficient habitat and thus have generally larger ranges than shallow water species both in terms of depth range and geographic range (Costello et al., 2011). The primary data for this pattern comes from fish rather than benthic invertebrates, therefore it may not be valid to infer a global generalization. Indeed, patterns in bathymetric

MOLLUSKS IN THE DEEP SEA

General perception of marine mollusks is naturally driven by our access to shallow marine species commonly found on beaches and the history of shell collecting. The species and varied ecosystems found in the deep sea are less familiar to non-specialists.

The deep oceans represent a broad variety of habitats and ecosystems, distributed across a three-dimensional volume of water that represents over 90% of the habitable space on Earth (Costello et al., 2010; Rex and Etter, 2010). Mollusks inhabiting the ocean floor cover its entire range, from shallow coastal environments to the deep sea. The characteristics of the deep sea vary geographically, for example the depths of thermoclines, insolation, and lysoclines (depth of carbonate saturation), vary latitudinally and between ocean basins (Rex et al. 2000; Steele et al. 2009). These physical and chemical

ranges in the pelagic realm are very similar to latitudinal ranges of terrestrial groups (Brown et al., 1996). Deep-sea benthic habitats are heterogeneous and represent landscapes that vary on scales of hundreds of kilometers (Levin et al., 2001), which is not dissimilar to the magnitude of some continents. As a result, how many deep-sea species are endemic to the specific area where they were discovered, or simply have only been found there because of poor sampling, remains highly debated.

Apart from this overall diversity on the undersea mountains, valleys, and plains, there are oases that host astonishing high-density biomass in chemoautotrophic-based ecosystems. Geothermal energy is the foundation for hydrocarbon “cold” seeps and hydrothermal vents, or direct nutrient input can come from organic falls (such as whale carcasses and wood). All represent high-quality energy input to the deep-sea ecosystem constrained at a very small spatial scale (Gage and Tyler, 1992).

Food chains building on chemoautotrophic microbes form a suite of specialist animal species that is unique to each type of ecosystem. Specialist vent endemic species cannot live in other deep-sea sites such as whale falls (Wolff, 2005), and there is little overlap in vent and seep fauna. There are some ecological similarities among these “oases”, and some larger evolutionary radiations such as bathymodioline mussels or lepidopleuran chitons include species that colonize different deep-sea habitats (Thubaut et al., 2013; Sigwart, 2016), but each species is restricted to its own specialism.

At hydrothermal vents, seawater circulating through the seafloor is heated and enriched with reduced compounds; when the fluids emerge back into the main ocean, minerals precipitate around the fluid flow, often creating characteristic chimneys or “black smokers”. Images of these habitats show the vertical walls of the chimneys teeming with life (Figure 1), and the vent ecosystems are dominated by relatively few species occur-

ring in very high biomass, comparable to the density of life supported by tropical coral reefs (Van Dover, 2000).

The gastropods living in vent ecosystems include a large number of endemic lineages (McArthur and Tunnicliffe 1998), including unusual recently-derived adaptations such as the “scaly-foot” gastropod (*Chrysomallon squamiferum* Chen et al., 2015) in the Indian Ocean (Chen et al., 2015a). Each mollusk species lives in a “Goldilocks zone” (not too hot and not too cold) with very narrowly defined limits of temperature and ocean chemistry, somewhere on the gradient where mineral-rich superheated vent fluid emerges at over 300°C and is rapidly cooled by surrounding seawater at around 2°C. Species’ varying tolerances for temperature and acidic vent fluid create patches or zones dominated by particular taxa, much like the zonation in rocky intertidal shores (Van Dover, 2000).

Hydrothermal vents were first discovered in 1977 (Lonsdale, 1977; Van Dover, 2000). The identification of these self-contained ecosystems at 2550 m depth on the Galápagos Rift was a sea change for biology. Much of our knowledge about vent systems in general, is based on generalizations predicted from these earliest-discovered and best-understood sites. Since then, other vent sites, hosting different specialist communities, have been discovered in every ocean and more remain to be found (Rogers et al., 2012). Vents are known to occur at all actively spreading ocean ridges, back-arc basins, and some seamounts. Here we consider the impact of the advance of knowledge about deep sea ecosystems on our understanding of molluscan biodiversity and its conservation.

HYDROTHERMAL VENTS, FAST AND SLOW

The tectonic geology of the seabed is different, in different ridge systems around the globe. There are at least



Figures 1–2. The Kairei Vent Field, Central Indian Ridge. **1.** Overview of the Monju site in the Kairei Vent Field, the foreground is covered by anemones, the spires of chimneys are covered by dense aggregations of vent shrimp (one seen swimming in foreground). **2.** *Chrysomallon squamiferum* from the Kairei Vent Field, shell length = 39.1 mm.

11 distinct biogeographic provinces among vent systems along the mid-ocean ridges and back-arc spreading centers of the global seafloor (Rogers et al., 2012). The distribution of animals among these widely separated habitats is largely explained by the local sea-floor spreading rates (Tunnicliffe and Fowler, 1996). Fast-spreading centers such as East Pacific Rise (EPR) have rapidly forming black smoker chimneys that are prone to collapse and re-grow on sub-decadal timescales (Shank et al., 1998); slow spreading centers, such as the Southwest Indian Ridge, may have physical vent structures and communities that are stable over multi-decadal or even much longer timescales (Lalou et al., 1990). Vent fields that are close to each other, on a scale of hundreds of kilometers apart, have similar but often non-identical species assemblages (Van Dover, 2001) whereas vent systems on different ocean ridges represent entirely different faunas (Ramirez-Llodra et al., 2007; Rogers et al., 2012).

The majority of detailed studies come from EPR and the mid-Atlantic ridge, which are distinctly different from all other global vent fields in terms of their fauna, biogeography, dispersal potential, and spreading rates of the underlying geology (Van Dover et al. 2002). The first exploration of vent fields in the Indian Ocean showed relatively minor differences in underlying geology compared predicted patterns, but dramatically different fauna (Van Dover, 2001).

Despite these clear differences, the uniquely fast turnover of the EPR fauna seems to be the basis of generalizations about hydrothermal vent ecosystems. Other vent systems, with slower turnover, are inevitably more sensitive to and much slower to recover from any disturbance.

Conservation of the deep sea, including hydrothermal vents, must account for the modern understanding of geographical variation in ecosystems. Hydrothermal vents occur even at the slowest spreading portions of global mid-ocean ridges such as the Southwest Indian Ridge and the Arctic Ocean (Tivey, 2004; Pederson, et al., 2010). Slower spreading seems to correlate with more stable faunal communities, low natural disturbance, and probably higher sensitivity and slower recovery from disturbance (Van Dover, 2014); however, these same slow-spreading centers may also generate comparatively large mineral deposits (Tao et al., 2014). Thus the most sensitive areas are the primary target for commercial exploitation. And the assessment of the potential damage of that exploitation is inferred from a dissimilar system.

Individual vent fields vary in scale but tend to be at most a few kilometers across. Images of dense biomass can be misleading, as the surrounding context of empty ocean is never visible. Some iconic vent sites are actually tiny; the Kairei Vent Field on the Central Indian Ridge, where the scaly-foot gastropod was first discovered, covers an area 80×30 m, less than half the size of a football field (Van Dover, 2001). Contrast this to feasibility studies, which have shown that current demand

for rare earth minerals for only one year's global consumption requires extraction of 5 km² of seabed (Kato et al., 2013). That represents mining activity over more than 2000 times the size of the entire Kairei Vent Field, every year.

It is unclear whether the value of the minerals extracted could ever offset the extreme cost and risk of deploying mining equipment to the deep sea, and the environmental damage caused to the seabed.

DEEP-SEA MINING

The United Nations (1994a) Convention on the Law of the Sea (UNCLOS) laid boundaries for the control of coastal access and coastal resources. Territorial waters of each nation extend only 12 nautical miles (22.2 km) from the low-water mark of its coastline, and the Exclusive Economic Zone (EEZ) extends beyond that to a further distance of up to 200 nautical miles (370.4 km). Within this region (and some additional distance where the continental shelf extends beyond the 200 nautical miles limit), each country holds control of the seabed and the pelagic realm for mining, fishing, and other activities. Beyond that limit, the great majority of the area and volume of the Earth's oceans, are "international waters", the high seas, *mare liberum*: belonging to no-one and everyone. All states have equal freedom of passage, fishing, and access for research in international waters.

The legal control of the oceans is defined by distance from land, not by depth. What constitutes "deep" sea is not strictly defined, and the physical properties of seawater at depth (solar penetration, temperature, oxygen, current speeds) vary in different parts of the globe, but a minimum of 1000 m is generally accepted as biologically "deep" (Gage and Tyler, 1992). Coastal shells that are familiar in commercial trade come from near shore—even collectible species that are colloquially referred to as "deep water" are almost all captured within the exclusive economic zone of the country of origin. For example, many species and forms of *Zoila* spp. from Australia are sold as "deep water" cowries, but live mainly within the limits of deep human diving, to a maximum depth of perhaps 300 m (Lorenz and Hubert, 2002). Most people think of *Nautilus* spp. as "deep-sea shells", yet their shells actually implode at depths of around 750–900 m (Kanie and Hattori, 1983; Vermeij, 1993). The family Pleurotomariidae or "slit shells" is famous as a group of generally rare and collectible "deep-sea" gastropods, but their bathymetric range only extends to a maximum just shy of 1000 m (Harasewych, 2002).

We may think of the high seas as inaccessible, and not available for commercial exploitation, apart from the rather transient activities of shipping and fishing. The seafloor of the "free seas" may seem both practically and financially remote, and under the implicit protection of the United Nations. In implementing the Convention on the Law of the Sea (United Nations, 1994a), the United

Nations (1994b) established the International Seabed Authority (ISA) exactly to administer access to the floor of the ocean beyond states' jurisdiction (Jaeckel, 2015). The text of the original UN resolution includes the statement that it was:

"Reaffirming that the seabed and ocean floor . . . are the common heritage of mankind, Mindful of the importance of the Convention for the protection and preservation of the marine environment and of the growing concern for the global environment . . ." (United Nations, 1994b: 3)

In July 2016, the ISA published a full working draft of exploitation regulations to govern the active extraction of minerals from mining the seabed in the high seas (ISA 2016). Exploration for commercial deep-sea mining is already well underway. The first set of 15-year licenses for mining exploration issued by the ISA to governments and commercial mining interests have already expired. Exploration licenses were granted to seven different groups from Europe, Russia, Korea, China, Japan, and India, with contracts starting in 2001–2002, and all have applied for contract extensions. The challenge for the ISA is to balance commercial pressures with a mandate to manage conservation, in a data limited environment and a largely untested legal framework (Jaeckel, 2016).

The reality of deep-sea mining, including heavy machinery deployed to the abyss, seems to stand in stark contrast to the unexplored inaccessible mysteries of the deep. But the technology is rapidly advancing, driven by potential access to valuable rare minerals, and international competition for first access to a new commercial frontier (Hoagland et al., 2010; Aldhous, 2011). The key targets of seabed exploitation are polymetallic nodules, polymetallic sulfides, and cobalt-rich ferromanganese crusts. Sulfides, rare earth minerals, and rare metals, including cobalt, are found in high densities at sites of geological spreading activity, such as hydrothermal vents (Tao et al., 2014; Van Dover, 2014).

The vivid images of dense communities and biomass at hydrothermal vents, in an ecosystem with no sunlight, are now a familiar part of deep-sea biology. The geological setting of vents creates habitat, small oases in the deep sea dependent on geothermal energy, but also exploitable concentrations of mineral deposits. Thus, vent areas globally became focal points for both conservation concerns and commercial exploitation. This conflict has been dismissed in many studies, based on misunderstanding of the diversity of vent geology and vent biota.

OUT OF SIGHT, BUT NOT OUT OF MIND

There are important reasons that prevent deep-sea mollusks from direct commercial exploitation for the shell collecting trade. Publicly funded scientific expeditions are currently the only mechanism for collecting

these shells in most localities. To ensure the protection, preservation, and inclusive scientific access to this precious material, they belong in permanent, publicly available museum collections, not in the control of individual researchers or private citizens. Public education about these animals is also crucial to their future survival. A disconnect between scientists and mollusk enthusiasts may be to the detriment of conservation efforts.

We consider the scaly-foot gastropod, *Chrysomallon squamiferum* (Chen et al., 2015a: Figure 2), as a case study of an animal that is popular and well-known, but that lacks protection or detailed study in its own hydrothermal vent habitat. The scaly-foot gastropod is an iconic member of the Indian Ocean hydrothermal vent fauna, known for the mineralized scales that cover the outer surface of its foot (Chen et al., 2015b). This species has been reported from only three sites since its discovery in 2000. Its total habitat covers less than 0.02 km² or less than one-fifth of a football field in total range, spread over an area of nearly 1,000,000 km² (925,347 km²) (Figure 3).

Among the three sites where the scaly-foot has been reported, two are located in Area's Beyond National Jurisdiction (ABNJ) and therefore fall under the legal mandate of the ISA. The Solitaire Vent Field occupies an area of 50×50 m and is within the EEZ of Mauritius (Nakamura et al., 2012). The Kaïrei Vent Field is of very similar size, at around 30×80 m (Van Dover et al., 2001), but 773 km south of Solitaire, the entire area of Kaïrei Vent Field is under an active mining exploration license granted to Germany (2015–2030) by the ISA. The third, southernmost reported population is located 2563 km to the southwest, at Longqi Vent Field. There, the main vent field spans 100×150 m (Tao et al., 2014), and this and the surrounding areas are under a mining exploration license granted to China (2011–2026). The conservation status of this species has not yet been assessed by the IUCN, although a population genetic study examining the connectivity among the three populations revealed poor connectivity between Longqi and the other two populations, implying dispersal barrier exist across the two ridges (Chen et al., 2015c). There are no conservation measures in place, and none have yet been proposed, for any of these sites.

Each hydrothermal vent site, especially those in the remote Indian Ocean, are observed on average less than once a year by the collective global endeavor of scientists, and independent monitoring of any commercial activity in such sites is nearly impossible. There is a small island in the River Thames, UK, designated as a nature reserve to protect terrestrial snails and other wildlife (Burns et al., 2013). At 9 acres (0.035 km²), Isleworth Ait is almost twice the area of the entire known habitat for *Chrysomallon squamiferum*, and this island is not the only reserve for the two-lipped door snail *Alinda biplicata* (Montagu, 1803). Additional protection for deep-sea biota would seem to be warranted.

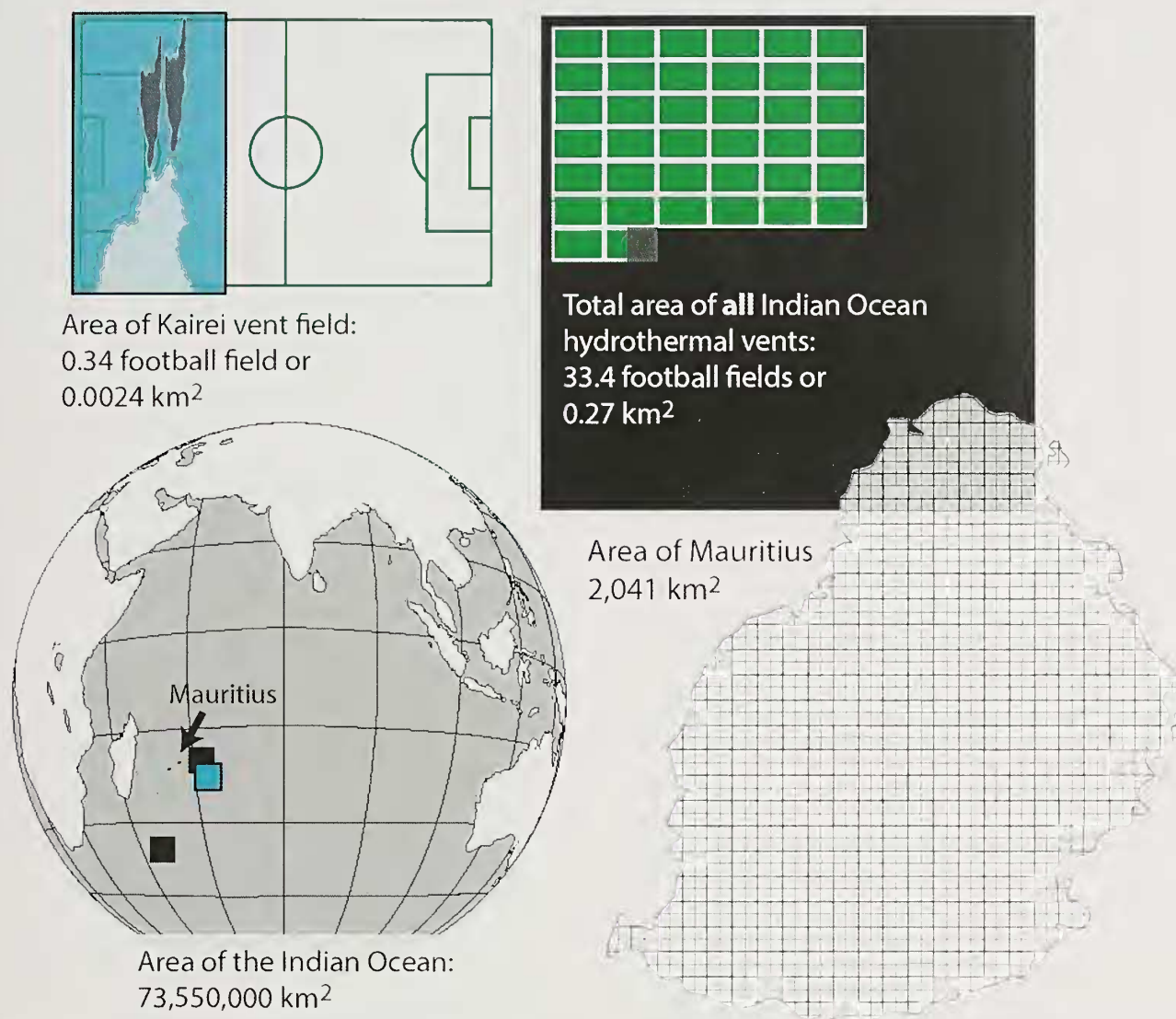


Figure 3. Infographic depicting the relative scale of hydrothermal vent sites. Top left, the area of Kairei Vent Field on the Central Indian Ridge is shown as the blue box relative to a sports field conforming to regulations of Fédération Internationale de Football Association (FIFA), 105×70 m. Top right, the sum of all Indian Ocean hydrothermal vent fields, represented to scale in green playing fields, against an 1 km^2 black square. This area was calculated based on a count of 37 reported Indian Ocean sites of vent activity according to the InterRidge international database, and an arithmetic average size of 7225 m^2 per vent field, based on the four well-mapped confirmed active sites (Edmond, Kairei, Solitaire, Longqi). The island of Mauritius is shown with approximately 1-km grid squares. At bottom left, the map of the Indian Ocean compares the location of Mauritius and the three vent sites where the scaly-foot gastropod, *Chrysomallon squamiferum*, has been found (Solitaire, Kairei in blue, and Longqi; boxes not to scale).

There are more than 712 animal species described from hydrothermal vents, in only 40 years since the first dramatic discovery of these ecosystems (Wolff, 2005). Among these are more than 250 mollusk species and that number is continuously increasing. Study of hydrothermal vents changed thinking about the limits of life on earth, expanding to a world without solar energy (Van Dover, 2000). This has expanded scientific knowledge but also enriched the understanding of our planet for everyone. Scientists and citizens alike have a role to voice concern over potentially permanent damage to the deep oceans.

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